

BIOLOGY OF *OIDEMATOPS FERRUGINEUS*
(DIPTERA: SCIOMYZIDAE), A PARASITOID ENEMY OF
THE LAND SNAIL *STENOTREMA HIRSUTUM*
(MOLLUSCA: POLYGYRIDAE)

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Abstract.—The biology of *Oidematops ferrugineus* Cresson and its association with the common woodland snail *Stenotrema hirsutum* (Say) is discussed.

The acalyptate dipterous family Sciomyzidae consists of approximately 600 species distributed in nearly all of the world's faunal regions. Over 150 species have been recorded from North America. Thanks to the long-continued efforts of C. O. Berg and a host of his students at Cornell University, the basic biology of the family is now quite well known. The larvae are predators or parasitoids of snails, snail eggs, slugs, and finger-nail clams (Berg and Knutson, 1978). Because of their predaceous habits, several of the aquatic species may have value in the biological control of medically or agriculturally important snails (Berg, 1973; Chock et al., 1961; Pettijean, 1966).

Most Sciomyzidae have aquatic or subaquatic larvae and are commonly abundant in wetland habitats. In contrast, surprisingly few of the Nearctic species occur in truly terrestrial environments. Adults of these species, about 12 in number, are usually encountered in mesic woodlands where their larvae prey on land snails (Bratt et al., 1969; Foote, 1961) or slugs (Trelka and Foote, 1970). A somewhat smaller number of species are found in marshy habitats but have larvae that prey on terrestrial pulmonate gastropods, particularly succineid snails (Berg, 1953; Bratt et al., 1969; Foote, 1959b, 1961). A distinct trend towards increasingly intimate associations with the molluscan prey is correlated with the ecological shift from aquatic to terrestrial habitats (Berg et al., 1959).

During the spring of 1966, puparia of an unrecognized species of Sciomyzidae were discovered in empty shells of the common woodland snail *Stenotrema hirsutum* (Say) (Polygyridae). Adults reared from these puparia proved to be *Oidematops ferrugineus* Cresson, a very rare and biologically unknown species. During subsequent rearings, the life cycle and larval feeding habits have been elucidated. Discovery of the larvae of *Oidematops* fills in the last remaining gap in our biological knowledge of genera of the tribe Sciomyzini in North America.

Other genera of Sciomyzini for which life history data are available are *Atrichomelina* (Foote et al., 1960), *Colobaea* (Knutson and Bratt, in prepara-

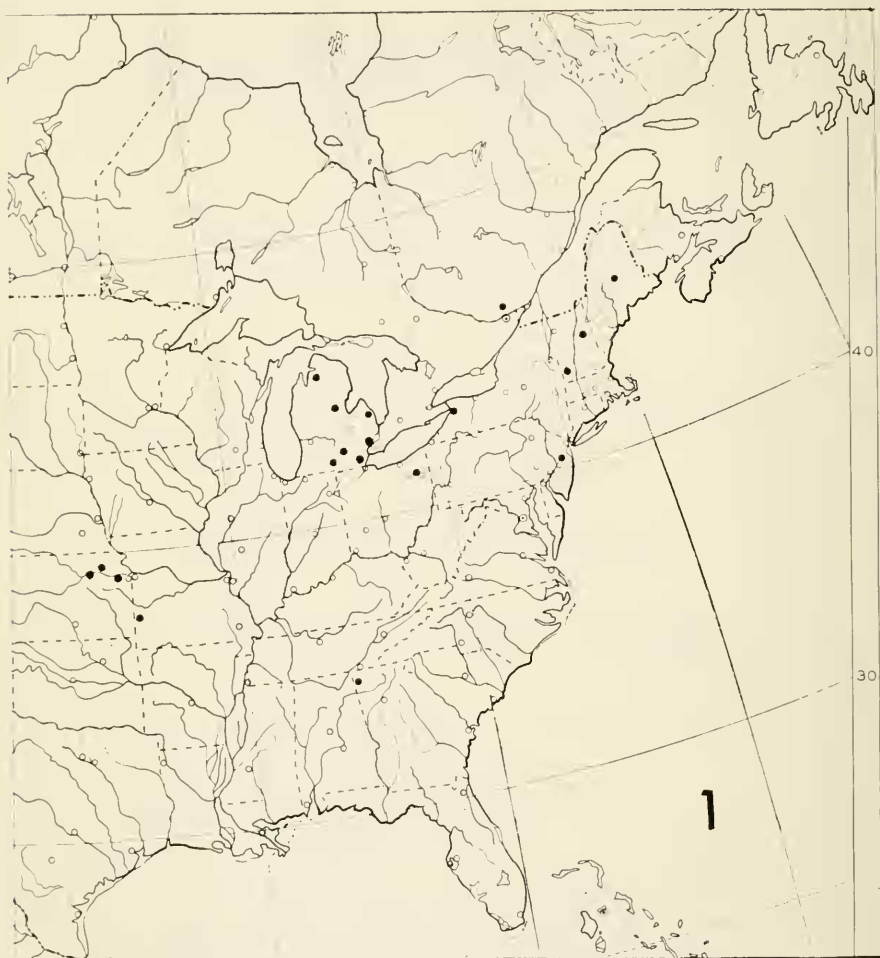


Fig. 1. Distribution of *Oidematops ferrugineus*.

tion), *Pherbellia* (Berg, 1953; Bratt et al., 1969; Foote, 1973), *Pteromiera* (Rozkošný and Knutson, 1970), and *Sciomyza* (Berg, 1953; Foote, 1959a). Of the 20 recognized genera of Nearctic Sciomyzidae, only *Dictyacium* and *Poecilographa*, both members of the tribe Tetanocerini, remain unknown biologically.

The strictly Nearctic genus *Oidematops* was originally proposed by Cresson (1920) for his new species, *ferrugineus*, the type-specimen of which was collected by C. W. Johnson at Manchester, Vermont in 1910. The genus has remained monotypic until the present time. It belongs to the tribe Sciomyzini of the subfamily Sciomyzinae (Steyskal, 1965) and probably

is relatively close phylogenetically to the genus *Sciomyza*. It is distinguished from other genera of Sciomyzidae by the following combination of characters: Propleural bristle well developed, fore tibia with 2 pre-apical bristles, arista white, 1 orbital bristle, post humeral bristle absent.

Adults of *Oidematops ferrugineus* are shining reddish brown in color; range in length from 6.5 to 8.5 mm; have slightly darkened, unpatterned wings; a distinctly protruding facial region; and a white arista.

The distribution of *O. ferrugineus* (Fig. 1) is eastern and midwestern, with records available for Georgia, Kansas, Maine, Michigan, Missouri, New Hampshire, New Jersey, New York, Ohio, Vermont and Quebec. The range of the fly corresponds fairly well with that of the host snail, *Stenotrema hirsutum*, which occurs from eastern Canada to Georgia and west to Minnesota, Kansas, and Mississippi (Burch, 1962; LaRocque, 1953).

The present paper includes information on the life cycle and larval feeding habits of *Oidematops ferrugineus* and discusses the ecological relationship of this taxon to other North American Sciomyzidae that attack terrestrial gastropods.

Life History

In northeastern Ohio, *O. ferrugineus* was found only in lowland deciduous woods dominated by such tree species as American elm (*Ulmus americana* L.), silver maple (*Acer saccharinum* L.), and black cherry (*Prunus serotina* Ehrhart). Herbaceous vegetation present in the area during late May was somewhat hydrophilic and dominated by skunk cabbage (*Symplocarpus foetidus* (L.) Nuttall). A few small vernal pools were present, although *Stenotrema* snails harboring overwintering puparia were rarely, if ever, found in the wetter sites. According to Baker (1939), *Stenotrema hirsutum* "is one of the commonest and widely distributed snails in Illinois. Its usual habitat is in forests along river valleys where there is a growth of oak, hickory, elm, basswood, and box elder trees. The snail is found under and in old logs and under forest debris It seems to prefer moist locations, but has been found in some places which are relatively dry." Leonard (1959) states that "*Stenotrema hirsutum* is a characteristic snail of humid, forested regions." Other species of Sciomyzidae collected in the habitat were *Poecilographa decora* (Loew), *Euthycera arcuata* (Loew), and *Tetanocera rotundicornis* Loew.

Judging from the few collection records available, the adult flight period extends from late May to early July. Adults were not encountered in nature in northeastern Ohio, but rearing records indicate that the flight period is about one month. Emergence occurs in late May, and mating and oviposition take place during the first two weeks of June. Two females that emerged from overwintering pupae collected in nature lived

in the laboratory for 25 and 26 days, respectively. The premating period for these two females was two and three days. No overt courtship behavior was observed, and mating attempts seemed to be of the assault type. The mating position resembled that described for many other species of the tribe Sciomyzini (Bratt et al., 1969). The copulatory act lasted from less than 20 minutes to well over an hour.

The preoviposition period, from emergence of a female to her first egg-laying activity, varied from 3–5 days. Nearly mature eggs were present in the ovaries of newly emerged females. That unfertilized females will oviposit is shown by the fact that an unmated female that emerged on 20 March 1966, deposited 84 inviable eggs before dying on 10 April. Mated females were more fecund, and three females that emerged in late April and early May produced 194, 272, and 322 eggs, respectively. The oviposition period for these three females ranged from 8–22 days and the daily egg production for a female varied from 0–56. The female that lived only 8 days averaged 24.2 eggs/day, the one living 20 days produced an average of 16.1 eggs/day, and the female that lived 22 days averaged 12.4 eggs/day. There was no noticeable decline in the number of eggs laid per day as the three females aged. Thus, one female deposited 32 eggs, another produced 27, and the third laid 25 eggs during the day preceding death. Eggs were attached to various sites in the breeding jar, although most were placed on projecting sprigs of the peat moss that formed a moist substrate in the jars. Of the 788 eggs deposited by the three fertilized females, approximately 750 were placed on the peat moss. The remaining eggs were placed singly or in groups of 2–5 onto shell fragments of dead *Stenotrema* snails, the glass walls of the breeding jars, and the cheesecloth covers. No eggs were placed on the shells of living *Stenotrema*. Eggs were not arranged in distinct clusters and were not affixed to the substrate by a mucilaginous secretion. They were easily removed by use of a moistened brush. The eggs possessed no unusual features in the chorionic markings and resembled quite closely eggs of numerous species of *Pherbellia*. The incubation period varied from 4–14 days and averaged 6 days.

Newly hatched larvae were quite active and moved steadily, if erratically, over the substrate. They paused frequently and changed direction repeatedly but, in contrast to the slug-killing larvae of *Tetanocera plebeia* Loew (Trelka and Foote, 1970), rarely lifted the anterior part of the body away from the substrate. They did not show a tendency to crawl up vertical surfaces but did avoid drier areas in the rearing dishes, and they moved away from areas illuminated by a microscope lamp. No burrowing habits were noted, and larvae generally remained on the surface of the peat moss substrate as long as moisture was present.

Upon contacting an active or retracted snail, the larva paused and applied its anterior end to the edges of the snail's foot or mantle. If the

snail was *Stenotrema hirsutum*, the larva quickly crawled into the aperture of the shell and attempted to insert itself between the flesh and the columella. Larvae that encountered snails other than *S. hirsutum* did not attempt to move into the aperture and quickly resumed their wandering movements over the moist substrate. Larvae failed to invade *Catinella avara* (Say), *Oxyloma* sp. (Succineidae), *Ventridens demissus* (Binney) (Zonitidae), *Haplotrema concavum* (Say) (Haplotrematidae), and *Triodopsis multilineata* (Say) and various other unidentified immature individuals of the family Polygyridae, all species that occurred in the larval habitat. They also failed to attack *Arion* and *Deroceras* slugs and showed no interest in gastropod eggs. Larvae that successfully invaded *Stenotrema* always assumed a position between the flesh of the snail and the shell, although many larvae shifted their locations frequently. Larvae usually positioned themselves so that their posterior spiracles were exposed to air in the aperture of the shell, although a few larvae moved deeper into the shell and thus lost contact with the aperture. Most of the latter larvae failed to survive beyond the first instar and could be found several days later as dead individuals flattened against the shell. Multiple attacks by newly hatched larvae were common, and as many as four larvae were found in a partly retracted snail. None or only one of the multiple larvae survived to form puparia, and very few managed to reach the second instar. Successful development to the pupal stage even by singly infesting larvae was rare. Although approximately 150 living *Stenotrema* were attacked by newly hatched larvae in the laboratory rearings, only 19 puparia were obtained. This is a success rate of 13%. Mortality was highest among first-stage larvae, either because they failed to invade a *Stenotrema* or because they were unable to maintain themselves in the snail. Several of the latter apparently were forced to leave the snail because they were one of 2-4 larvae that had originally infested the host. Practically none of these larvae managed to invade a second snail. Other larvae died in the second or third instar mostly because of the premature death of the snail. Larvae that survived until at least halfway through the third stadium in a living host could withstand death of the snail and complete larval life as scavengers, feeding on the decomposing snail tissues. In contrast, younger larvae quickly succumbed once their host expired. Strangely, most of these larvae made no attempt to abandon the dying or dead snails but instead remained within the liquifying tissues. These larvae usually died within 1 or 2 days following death of the host. Many first instars, even if they were the sole invaders of a *Stenotrema*, failed to retain their position within the snail and could be found a few days later entrapped in a ball of mucus lying on the substrate. Perhaps the mortality rate of larvae reared under laboratory conditions was higher than that of larvae hatching under natural conditions due to the greater activity of the snails that were held under constantly humid conditions. *Stenotrema* snails in nature

probably are relatively inactive during the daylight hours, thus allowing easier entrance and establishment of newly hatched larvae. However, an argument against the idea of a higher mortality rate in laboratory-reared larvae is the fact that only 10 puparia were found in 150 *Stenotrema* snails collected in nature on 23 March 1966. This is an infestation rate of 6.6%, a figure distinctly below the 13% success rate obtained in the laboratory rearings.

Larvae fed by scraping the flesh of the snail with their sharply pointed mouthhooks. The mouthhooks apparently worked in conjunction with the anteriorly toothed ventral arch, located below the mouthhooks, to rip and tear pieces of flesh from the snail's mantle. Later, the foot and internal organs were attacked and consumed. Destruction of the latter, of course, quickly caused death of the host. Snails containing only one larva usually remained alive and active for at least 6 days after being invaded by a newly hatched larva. They moved about the rearing dish, fed on provided lettuce, and seemingly were unaffected by the feeding of the slowly developing larva. However, 6–10 days after being initially attacked, the snails retracted into their shells and no longer crawled about the rearing dishes. A day or so later, they showed distress by exuding a milky mucus and developing waves of fine tremblings that passed over the surface of the retracted foot. The larva at this time was always in the second or third instar. Infested snails typically died 4 or 5 days after becoming retracted, at which time the larva was in the third instar and quite sizeable. Between 12 and 16 days commonly elapsed from the original larval invasion to death of the snail host.

After death of the host, the third instar fed as a scavenger on the decomposing, rapidly liquifying snail tissues. It always kept its posterior end at the surface of the black, evil-smelling carcass and accompanying fluids with the result that the spiracles were in constant contact with air. Shortly before forming its puparium, each larva tended to clean the shell of remaining flesh by actively shoving the decomposed remains out of the shell aperture. The larva then reversed its position and formed a puparium in the body whorl of the shell. The anterior end of the puparium usually was located just behind the teeth that project from the wall of the body whorl into the lumen of the shell.

Although it was difficult to get accurate data on the duration of the 3 larval stadia, I estimate that the first stadium lasted about 4–5 days; the second, 6–8; and the third, between 10 and 12 days. The total larval period ranged from 20–25 days.

The prepupal period, from formation of the puparium to actual appearance of the pupa, ranged from slightly less than 24 hours to somewhat over 48 hours. Apparently growth and development quickly ceased in the newly-formed pupae, as none even developed eye pigment during the

several weeks that they were held at room temperatures. They entered a state of diapause that was broken only by exposing pupae to extended periods of low temperature.

Nineteen puparia containing apparently viable pupae were obtained in the laboratory rearings. No adults had emerged from these puparia after continuous exposure to room temperatures for periods varying from 26 (1 puparium) to 106 days (2 puparia). All puparia, still with apparently viable pupae, were subsequently placed in an unlighted refrigerator where they were held at 5–7°C for periods varying from 90–150 days. They were then returned to room temperatures. No emergence from these chilled puparia was obtained, an indication that the pupal diapause is quite intense.

In contrast to the failure of laboratory-reared pupae to break diapause, a puparium collected in nature on 14 September 1965, finally produced an adult female on 20 March 1966. The puparium had been placed in a dark refrigerator on 20 October 1975, where it remained until 1 March 1976, a lapse of 165 days. This rearing suggests that longer exposures to low temperatures than the 90–150 days given the laboratory-reared individuals is necessary to break diapause. Six of eight puparia collected in nature on 23 March 1966 produced adults in the laboratory within 31 days.

That a few pupae in each generation require at least two lengthy exposures to low temperatures before they will break diapause is suggested by the fact that two of the eight puparia collected on 23 March had not produced adults by 8 September 1966, after 169 days of continuous exposure to room temperatures. Both still contained apparently viable pupae at the end of the holding period.

All of the rearing records strongly suggest that *Oidematops ferrugineus* is univoltine. Adults emerge in late May and June, quickly mate, and begin ovipositing within 3–5 days. The incubation period is 4–14 days, and the larval period lasts approximately 22 days. Pupae are formed in early and midsummer; these quickly go into diapause and serve as the overwintering stage. Diapause appears to be obligatory and is broken by exposure to low winter temperatures. A few pupae in each generation may require at least two exposures to winter temperatures before renewing development and producing adults.

Apparently pupae of *O. ferrugineus* are occasionally destroyed by parasitoid wasp larvae, as a small emergence hole was found in a puparium collected in nature on 14 September 1965.

Ecological Relationship of *Oidematops ferrugineus* to Other Sciomyzidae that Attack Terrestrial Gastropoda

Table 1 lists the 22 species of Sciomyzidae that are known to prey on terrestrial Gastropoda in North America. Only records of gastropod genera

actually known to harbor larvae in nature are included; laboratory rearings utilizing other genera are deleted. The following discussion is restricted to woodland inhabiting species that could be potential competitors of *O. ferrugineus* for a possibly limited supply of land snails. Other species included in Table 1 either occur beyond the range of *O. ferrugineus* or are found in open marshes and thus are segregated by habitat.

Sciomyza aristalis Coquillett and *Tetanocera melanostigma* Steyskal are fairly common in lowland woods in the eastern states but are in a trophic niche distinctly different from that occupied by *Oidematops ferrugineus*. Both species are specialized parasitoids of snails belonging to the family Succineidae. Their larvae are highly host specific and have never been found in nature in any gastropod genera except *Succinea* and *Oxyloma*.

Pherbellia albocostata (Fallén) and *Pteromicra steyskali* Foote have been reared from species of *Discus*, a genus of the family Endodontidae. Thus these species also are utilizing a family of land snails different than that attacked by *Oidematops ferrugineus*.

Pherbellia albovaria (Coquillett) has been reared from a species of *Triodopsis*, a member of the Polygyridae, the same family to which *Stenotrema hirsutum*, the host of *Oidematops ferrugineus*, belongs. Although larvae of *Pherbellia albovaria* have not yet been found in *Stenotrema* it is reasonable to assume that this species occasionally could be in the same trophic niche as *Oidematops ferrugineus*. However, *Pherbellia albovaria* usually has been collected in mesic woodlands and has rarely been taken in the low, wetter forests favored by *Oidematops ferrugineus*. The two species are largely segregated by habitat, with the result that larval competition for a possibly limited snail resource is avoided or at least reduced.

Young larvae of *Tetanocera clara* Loew, *T. plebeia*, and *T. valida* Loew are restricted to slugs and thus would not be competing with *Oidematops* larvae for *Stenotrema* snails. However, older larvae of *Tetanocera plebeia* and *T. valida* are somewhat more generalized in their feeding habits and will attack *Stenotrema* under laboratory conditions. Possibly larvae of these two species at times utilize the same prey attacked by *Oidematops ferrugineus*.

The only sciomyzid that appears to be significant as a potential competitor of *O. ferrugineus* is *Euthycera arcuata*, a fairly common and widespread woodland-inhabiting species, whose larvae have been found in three genera of land snails, including *Stenotrema*. However, the two species appear to be somewhat temporally separated. *Euthycera arcuata* overwinters as a larva, whereas *Oidematops ferrugineus* passes the cold season as a pupa. *Oidematops* emerges as an adult in late May and early June, lays eggs within a few days, and completes larval development about a month later. In contrast, adults of *Euthycera arcuata* have not been collected in northeastern Ohio until late June and do not oviposit until

Table 1. North American species of Scionyzidae known to prey on terrestrial gastropoda.

Species of Scionyzidae	Genus of prey	Reference
Tribe Scionyzini		
<i>Scionmyza aristalis</i> Coquillett	<i>Succinea</i>	Foote (1959a)
<i>Scionmyza dryomyzina</i> Zetterstedt	<i>Oxyloma</i>	Berg (1953), Foote (1959a)
<i>Scionmyza simplex</i> Fallén	<i>Oxyloma</i>	Foote (1959a)
<i>Oidemotops ferrugineus</i> Cresson	<i>Stenotrema</i>	Present paper
<i>Pherbellia albocostata</i> (Fallén)	<i>Discus</i>	Bratt et al. (1969)
<i>Pherbellia albocaria</i> (Coquillett)	<i>Discus, Anguispira, Zonitoides, Triodopsis</i>	Bratt et al. (1969)
<i>Pherbellia schoenherri maculata</i> (Cresson)	<i>Succinea, Oxyloma, Catinella</i>	Bratt et al. (1969)
<i>Pteromicra anopla</i> Steyskal	<i>Succinea</i>	Steyskal (1954)
<i>Pteromicra perissa</i> Steyskal	<i>Pupilla</i>	Steyskal (1958)
<i>Pteromicra steyskali</i> Foote	<i>Discus</i>	Foote (1959b)
Tribe Tetanocerini		
<i>Euthycera arcuata</i> Loew	<i>Mesodon, Stenotrema, Ventridens</i>	Foote (unpublished rearings)
<i>Hoplodictya acuticornis</i> (Wulp)	<i>Succinea</i>	Fisher and Orth (1972)
<i>Hoplodictya spinicornis</i> (Loew)	<i>Oxyloma, Succinea</i>	Neff and Berg (1962)
<i>Tetanocera clara</i> Loew	<i>Pallifera, Philomycus</i>	Trelka and Foote (1970)
<i>Tetanocera melanostigma</i> Steyskal	<i>Succinea, Oxyloma</i>	Foote (1961)
<i>Tetanocera oxia</i> Steyskal	<i>Catinella</i>	Foote (unpublished rearings)
<i>Tetanocera phyllophora</i> Melander	<i>Discus</i>	Foote (unpublished rearings)
<i>Tetanocera plebeia</i> Loew	<i>Deroceras, Oxyloma</i>	Trelka and Foote (1970)
<i>Tetanocera rotundicornis</i> Loew	<i>Oxyloma</i>	Berg (1953), Foote (1961)
<i>Tetanocera spirifera</i> Melander	<i>Oxyloma</i>	Foote (unpublished rearings)
<i>Tetanocera valida</i> Loew	<i>Deroceras</i>	Trelka and Foote (1970)
<i>Trypetoptera canadensis</i>	<i>Vallonia</i>	Foote (unpublished rearings)

several days later. As a result, its larvae do not even begin searching for prey snails until sometime in July, at a time when larvae of *Oidematops ferrugineus* are reaching maturity and beginning to form puparia. Therefore, it is very doubtful if these two species, although occupying the same trophic and spatial niches, are actively competing for the same snail resource. Larvae of *Euthycera arcuata* probably attack only those individuals of *Stenotrema* that are missed by larvae of *Oidematops*. Further, *Euthycera* is more of a trophic generalist than *Oidematops* in that its larvae can attack a wider spectrum of terrestrial gastropods. Thus, only part of its larval population utilizes *Stenotrema* snails, considerably reducing the impact of this species on the highly host specific *Oidematops*.

It is quite possible that additional families of cyclorrhaphous Diptera contain species that prey on *Stenotrema* and thus trophically at least are ecological equivalents of *O. ferrugineus*. Very little work has been directed towards these other malacophagous species, but it is known that a few species of *Sarcophaga* (Sarcophagidae) have larvae that prey on land snails belonging to the family Polygyridae (Dodge, 1956). So far, however, none has been reared from any species of *Stenotrema*.

Based on the evidence available, it appears that *Oidematops ferrugineus* has invaded a niche that is relatively unoccupied by other species of Diptera. Of course, its high degree of host specificity has both advantages and disadvantages. By specializing on land snails of the genus *Stenotrema*, *Oidematops* has evaded competition from other malacophagous species. On the other hand, its trophic inflexibility makes it vulnerable to any environmental disruption that might reduce populations of its larval host.

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